# Gross primary productivity and respiration in the experimental wetland basins, 1996-98

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# Introduction

Primary production and respiration, collectively referred to as metabolism, are functions which are particularly important as indicators of the general state of an ecosystem. These biological processes, in turn, influence a number of physical and chemical characteristics in aquatic ecosystems (Buffle and DeVitre, 1994). The influence of aquatic metabolism is particularly pronounced in shallow-water ecosystems such as wetlands, where the euphotic zone is often restricted to a few centimeters depth (Cronk and Mitsch, 1994a,b; Mitsch and Gosselink, 1993). Water column metabolism in wetlands is associated with many important characteristics of the water column including species composition and diversity, turbidity, dissolved oxygen, nutrient biogeochemistry, pH, carbon dioxide, conductivity by stimulating precipitation, and temperature by shading and turbidity effects (Mitsch and Gosselink, 1993). As an ecosystem matures, it often ameliorates the harsher effects of its physical environment such as temperature and solar radiation, and biological feedback becomes a very important regulator of the ecosystem's biological, physical, and geochemical processes (Odum, 1969).

## Methods

From July 1996 to December 1998, four YSI 6000 (YSI Inc., Yellow Springs, Ohio) datasondes have been deployed in the two experimental wetland basins, one in each middle and outflow deepwater area (Figure. 1). These sondes were hung under wetland boardwalks so that the probes would be suspended in the middle of the water column. The sondes measured water temperature, pH, specific conductance, and dissolved oxygen at half-hour intervals. Sondes were removed from the wetlands, downloaded, maintained and calibrated monthly according to the manufacturer's instructions.

From the dissolved oxygen data, rates of gross primary productivity and respiration were determined using the diurnal oxygen curve method (Odum, 1956). The method is illustrated in Figure 2. The rate of change in dissolved oxygen was calculated for each half-hour time interval according to the equation:

$$\frac{dDo}{dt} = \frac{DO_2 - DO_1}{t_2 - t_1}$$
(1)

## where DO = dissolved oxygen, g m<sup>-3</sup> t = time, hr

Average respiration ( $R_{avg}$ ) was calculated from mean night respiration rates (for these calculations, 0:00 to 6:00 am was used, see Fig. 2) before (denoted 0:00-6:00am) and after (denoted 24:00-30:00 am) the day for each calculation, when it was clear that there was no residual effect of sunlight.

$$R_{avg} = -\left[\frac{dDO}{dt}\right]_{0:00-6:00,24:00-30:00}$$
(2)



Figure 1. Locations of YSI datasondes locations (x) in the two experimental marshes from July 1996-December 1998. One datasonde was placed in each middle subbasin, and one in each outflow subbasin. Deepwater (0.35 m) areas are shaded.



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Figure 2. Illustration of the method used to estimate gross primary production (GPP) and respiration (R) (Odum, 1956). Dissolved oxygen (DO) readings are used to determine the rate of change for DO during the day, while both photosynthesis (P) and respiration(R) are occurring, and at night, when it is assumed that only R is occurring. The nighttime data points are used to determine the rate of R, shown in b) by a dotted line. The rate of R is added to the rate of change for DO and integrated over daylight hours to calculate GPP in g  $O^2 \text{ m}^3 \text{ d}^{-1}$ . This number is multipled by the average depth to determine areal GPP (c) in g  $O^2 \text{ m}^{-3} \text{ d}^{-1}$ .

Table 1. Gross primary production (GPP) and respiration (R) in research wetland basins at the Olentangy River Wetland Research Park, July 1996-December 1998. GPP and R were calculated using data taken every half-hour from four YSI 6000 data sondes (YSI, Inc., Yellow Springs, Ohio). W1 = Wetland 1 (planted), W2 = Wetland 2 (naturally colonizing).

	W1 Mide	dle	W1 Outflow		
Summer 1996 Fall 1996 Winter 1996-7	GPP, g $O_2 m^2 d^{-1}$ 4.30 ± 0.28(48) 1.92 ± 0.29(52) 0.36 ± 0.10(13)	R, g $O_2 m^2 d^{-1}$ 4.28 ± 0.26(48) 3.16 ± 0.38(52) 0.63 ± 0.12(13)	GPP, g $O_2 m^2 d^{-1}$ 5.70 ± 0.34(22) 2.94 ± 0.30(82) 0.99 ± 0.20(42)	R, g $O_2 m^2 d^{-1}$ 5.41 $\pm 0.44(22)$ 2.88 $\pm 0.28(82)$ 0.95 $\pm 0.20(42)$	
Spring 1997 Summer 1997 Fall 1997 Winter 1997-8	$\begin{array}{c} 0.70 \pm 0.23(12) \\ 4.35 \pm 0.43(77) \\ 2.13 \pm 0.28(74) \\ 0.93 \pm 0.08(80) \end{array}$	$\begin{array}{c} 0.60 \pm 0.23(12) \\ 4.39 \pm 0.42(77) \\ 2.12 \pm 0.27(74) \\ 0.96 \pm 0.06(80) \end{array}$	$\begin{array}{c} 1.60 \pm 0.11(75) \\ 4.80 \pm 0.53(50) \\ 1.40 \pm 0.18(70) \\ 0.72 \pm 0.08(75) \end{array}$	$\begin{array}{c} 1.64 \pm 0.12(75) \\ 4.84 \pm 0.52(50) \\ 1.49 \pm 0.19(70) \\ 0.82 \pm 0.07(75) \end{array}$	
Spring 1998 Summer 1998 Fall 1998 Average	$\begin{array}{c} 3.57 \pm 0.42(53) \\ 4.93 \pm 0.33(84) \\ 1.47 \pm 0.14(67) \\ 2.29 \end{array}$	$\begin{array}{c} 3.57 \pm 0.40(53) \\ 4.90 \pm 0.33(84) \\ 1.50 \pm 0.14(67) \\ 2.42 \end{array}$	$\begin{array}{c} 4.82 \pm 0.85(63) \\ 6.11 \pm 0.50(75) \\ 2.90 \pm 0.28(39) \\ 3.00 \end{array}$	$\begin{array}{c} 4.75 \pm 0.78(63) \\ 6.23 \pm 0.51(75) \\ 2.95 \pm 0.29(39) \\ 3.00 \end{array}$	
	W2 Middle		W2 Outflow		
	W2 Mide	dle	W2 Out	low	
Summer 1996 Fall 1996 Winter 1996-7	W2 Mide GPP, g $O_2 m^2 d^{-1}$ $5.35 \pm 0.36(40)$ $2.97 \pm 0.27(54)$ $0.57 \pm 0.12(11)$	dle R, g $O_2 m^{-2} d^{-1}$ 5.29 ± 0.35(40) 2.95 ± 0.25(54) 0.52 ± 0.13(11)	W2 Outfl GPP, g $O_2$ m <sup>-2</sup> d <sup>-1</sup> 5.95 ± 0.42(22) 2.13 ± 0.17(64) 1.57 ± 0.29(30)	How R, g $O_2 m^2 d^{-1}$ $5.94 \pm 0.42(22)$ $2.07 \pm 0.17(64)$ $1.68 \pm 0.25(30)$	
Summer 1996 Fall 1996 Winter 1996-7 Spring 1997 Summer 1997 Fall 1997 Winter 1997-8	$\label{eq:GPP} \begin{array}{l} \text{W2 Mide} \\ \text{GPP, g } O_2 \ m^2 \ d^{-1} \\ 5.35 \ \pm \ 0.36(40) \\ 2.97 \ \pm \ 0.27(54) \\ 0.57 \ \pm \ 0.12(11) \\ \end{array} \\ \begin{array}{l} 3.48 \ \pm \ 0.39(63) \\ 4.56 \ \pm \ 0.50(48) \\ 2.12 \ \pm \ 0.21(65) \\ 1.43 \ \pm \ 0.14(79) \end{array}$	dle R, g $O_2 m^2 d^{-1}$ 5.29 ± 0.35(40) 2.95 ± 0.25(54) 0.52 ± 0.13(11) 3.45 ± 0.39(63) 4.62 ± 0.48(48) 2.13 ± 0.20(65) 1.46 ± 0.13(79)	$\begin{array}{c} \mbox{W2 Outf}\\ \mbox{GPP, g } O_2 \ m^2 \ d^{-1}\\ 5.95 \pm 0.42(22)\\ 2.13 \pm 0.17(64)\\ 1.57 \pm 0.29(30)\\ 1.72 \pm 0.15(75)\\ 4.87 \pm 0.64(50)\\ 2.02 \pm 0.14(71)\\ 2.04 \pm 0.16(71)\\ \end{array}$	How R, g $O_2 m^2 d^{-1}$ 5.94 ± 0.42(22) 2.07 ± 0.17(64) 1.68 ± 0.25(30) 1.67 ± 0.14(75) 4.89 ± 0.63(50) 1.96 ± 0.16(71) 2.05 ± 0.16(71)	

where

 $R_{avg}$  = average respiration rate, g  $O_2 m^{-3} d^{-1}$ 

Instantaneous gross primary productivity was calculated by adding average respiration to the instantaneous rate of dissolved oxygen increase in dissolved oxygen during the day.

$$GPP_{inst} = dDO/dt + R_{avg}$$
(3)

where

 $GPP_{inst}$  = instantaneous rate of gross primary productivity, g O<sub>2</sub> m<sup>-3</sup> d<sup>-1</sup>

The total gross primary production was then calculated by integrating these rates over time for the day.

$$GPP_{vol} = \int_{dawn}^{dusk} GPP_{inst} dt$$
<sup>(4)</sup>

where

 $GPP_{vol} = total daily gross primary productivity,$  $g O_2 m^{-3} d^{-1}$  Total daily respiration was calculated by multiplying the average hourly rate of respiration by 24 hours.

$$R_{\rm vol} = 24 \, \rm hr/d * R_{\rm inst} \tag{5}$$

where  $R_{vol}$  = total daily respiration, g  $O_2 m^{-3} d^{-1}$ 

Equations 4 and 5 calculate GPP and R in terms of volume (g  $O_2 m^{-3} d^{-1}$ ). To convert this to an area basis, GPP and R were multiplied by the average depth of the deepwater basins (estimated from staff gage data measured twice daily) in order to express the results as g  $O_2 m^{-2} d^{-1}$ .

$$GPP = GPP_{vol}^* d_w$$
(6)

$$R = R_{vol}^{*} d_{w}$$
(7)  
where

GPP = total daily gross primary production, $g O_2 m^{-2} d^{-1}$ 

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R = total daily respiration, g  $O_2 m^{-2} d^{-1}$ d<sub>w</sub> = daily average water depth, m.

where GPP = total daily gross primary production,  $g O_2 m^{-2} d^{-1}$ R = total daily respiration,  $g O_2 m^{-2} d^{-1}$  $d_w$  = daily average water depth, m.

Net primary production was calculated from GPP and R:

 $NPP = GPP - R \tag{8}$ 

where

NPP= net primary productivity, g  $O_2 m^{-2} d^{-1}$ .

An oxygen diffusion correction was not considered in the estimation of metabolism for two reasons. First, the water column and surface in the wetland basins were completely covered with filamentous algae or duckweed, which act as physical barriers to diffusive transport across the air-water interface (see e.g. Morris and Barker, 1977), although it is recognized that some of the algae at the surface release oxygen directly to the atmosphere. Other researchers have found diffusion rates to be negligible in similar freshwater wetland ecosystems (Reeder, 1990, Mitsch and Reeder, 1991) because of the relative lack of surface turbulence.

GPP, NPP and R data were analyzed using a general linear model to determine which factors were statistically significant for each parameter measured. The main factors tested in the model were year, basin (1 or 2), season (spring, summer, fall, winter), and subbasin (middle, outflow). Interaction effects were also tested. For the purposes of the general linear model, spring was defined as March through May, summer as June through August, fall as September through Nov, and winter as December through February.



Figure 3. Summer gross primary production (GPP) in the middle subbasins of the experimental wetlands, 1996-98, expressed as a) annual averages for 3 years and b) individually by year. W1 = Wetland 1 (planted), W2 = Wetland 2 (naturally colonizing). W1 had significantly higher GPP in summer 1997 (paired t-test). Error bars indicate standard error. n = number of paired data points. Asterisks (\*) indicate significant differences between W1 and W2.

Table 2. Results of general linear models for GPP, R, and NPP in the experimental wetland basins at the Olentangy River Wetland Research Park, July 1996- December 1998.

GPP, g O <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>						
Source	df	Seq SS	Adj SS	Adj MS	F	р
year	2	265.14	362.47	181.23	22.87	0.000
season	3	4282.17	4058.55	1352.85	170.73	0.000
basin	1	28.58	43.70	43.70	5.51	0.019
subbasin	1	18.57	8.24	8.24	1.04	0.308
year*subbasin	2	123.31	102.95	51.48	6.50	0.002
season*basin	3	163.76	175.41	58.47	7.38	0.000
season*subbasin	3	97.23	80.75	26.92	3.40	0.017
basin*subbasin	1	43.60	43.60	43.60	5.50	0.019
Error	2312	18320.03	18320.03	7.92		
Total	2328	23342.38				
R, g O, m <sup>-2</sup> d <sup>-1</sup>						
Source	df	Seq SS	Adj SS	Adj MS	F	р
year	2	307.24	402.98	201.49	26.18	0.000
season	3	4156.16	3900.22	1300.07	168.89	0.000
basin	1	16.38	30.54	30.54	3.97	0.047
subbasin	1	8.21	0.14	0.14	0.02	0.891
year*subbasin	2	123.31	109.79	54.90	7.13	0.001
season*basin	3	176.98	184.56	61.52	7.99	0.000
season*subbasin	3	113.75	98.44	32.81	4.26	0.005
basin*subbasin	1	32.68	32.68	32.68	4.25	0.039
Error	2312	17797.00	17797.00	7.70		
Total	2328	22731.71				
NPP. a O. m <sup>-2</sup> d <sup>-1</sup>						
Source	df	Seq SS	Adj SS	Adj MS	F	р
year	2	2.60	1.35	0.60	1.04	0.355
season	3	1.34	2.68	0.90	1.37	0.250
basin	1	1.69	3.34	3.34	5.14	0.023
subbasin	1	2.09	7.43	7.43	11.43	0.001
year*basin	2	7.34	4.26	2.13	3.28	0.038
year*subbasin	2	13.84	12.79	6.40	9.84	0.000
season*basin	3	3.62	5.53	1.84	2.84	0.037
basin*subbasin	1	0.76	5.60	5.60	8.62	0.003
year*basin*subbas	in 2	14.79	14.79	7.39	11.38	0.000
Error	2311	1502.09	1502.09	0.65		
Total	2328	1550.15				

# **Results**

GPP and R showed strong seasonal patterns, with maxima in the summer and minima in the winter (Table 1). Net primary production was not significantly different from zero, except on two occasions (the middle subbasin of Wetland 1 in fall 1996 and winter 1996-7). The planted and unplanted wetlands were very similar in terms of aquatic metabolism. GPP and R were highest in the outflow subbasins; however, the middle subbasins occupy a much larger area and so have a greater impact in the system. GPP in the middle subbasins ranged from 0.36 g  $O_2 \text{ m}^{-2} \text{ d}^{-1}$  in winter to 5.35 g  $O_2 \text{ m}^{-2} \text{ d}^{-1}$  in summer. Summer GPP values in the middle subbasins ranged from 4.30 to 5.35 g  $O_2 \text{ m}^{-2} \text{ d}^{-1}$  (Table 1). Wetland 1 had significantly higher GPP in 1997, but the two wetlands were not significantly different in 1996 or 1998. A comparison of the three years of summer data as a whole also showed no significant difference between wetlands (Figure 3b).

ANOVA tables for GPP, R, and NPP are shown in Table 2. For GPP and R, the following factors showed significant (a=0.05) main effects: year, season, and

basin. Interaction effects were significant for year\*subbasin, season\*basin, season\*subbasin, and basin\*subbasin. Net primary production was explained by a different general linear model. The only significant main effects were for basin and subbasin, while five interaction terms were significant (year\*basin, year\*subbasin, season\*basin, basin\*subbasin, year\*basin\*subbasin). Analysis of the spatially detailed data showed that GPP and R were significantly higher in the deepwater areas of both wetlands than in the shallow areas.

## Discussion

The summer gross primary productivity in the fullscale wetlands  $(3.4 - 6.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1})$  was comparable to other productive temperate wetlands and hardwater lakes (Reeder, 1990; Vymazal, 1995). The GPP compared well with the range of 4.3 - 8.4 g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> observed in a coastal Lake Erie freshwater marsh (Reeder . 1990) and to seasonal averages of 2.2 - 6.4 g O2 m<sup>-2</sup> d<sup>-1</sup> obtained from constructed riparian wetlands in Illinois (Cronk and Mitsch, 1995b). When compared to eutrophic lakes, the areal gross primary productivity was very similar, indicating that even though the study wetlands are much shallower ecosystems, on an areal basis their productivity is equivalent to eutrophic lakes. The Fox Chain of Lakes in northeastern Illinois had areal GPP values of 1.0 - 9.6  $gO_2 m^{-2} d^{-1}$ , with an average value of 4.2  $gO_2 m^{-2} d^{-1}$ . GPP values for the wetlands were higher than for Lake Constance, Germany (0 -  $1.2 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ , Stabel 1988), even though the euphotic zone in that lake is 20 m deep. The large extent of primary production in a shallow water column leads to larger changes in water chemistry than would occur if the primary production were dispersed over a euphotic zone several meters deep, hence the large influence that aquatic primary producers have on the chemistry of the shallow wetland water column.

## Conclusions

Gross primary productivity (GPP) in the water column of highly productive temperate wetlands is similar, on an areal basis, to GPP values reported for eutrophic hardwater lakes, showing that despite an extremely shallow water column, wetlands can be as productive as these deeper aquatic ecosystems.

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